Early Cretaceous iguanodontians from East and Southeast Asia: new phylogeny and paleobiogeography

博士論文

Early Cretaceous iguanodontians from East and Southeast Asia: new phylogeny and paleobiogeography

（前期白亜紀の東・東南アジアのイグアノドン類：新しい系統と古生物地理）

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SUMMARY

I investigated the dinosaur fossils in the East and Southeast Asia in order to reveal the distribution pattern and evolution of dinosaurs during the Early Cretaceous. In particular, I focused on the iguanodontian dinosaurs because the Iguanodonita is the most common and diverse herbivores dinosaur and represented global distribution on the earth surface. I also described three specimens of iguanodontian dinosaurs obtained from the Lower Cretaceous of Japan, Thailand, and China. A new individual of *Probactrosaurus* from China was proposed, and detail descriptions of each skull bone were performed. The results of the present study are summarized below:

(1) I selected three Early Cretaceous sequences in Japan, China and Thailand. In Japan, the Kitadani Formation, the upper-most of the Tetori Group, consists mainly of shales and sandstones and is the most productive sequence for dinosaur fossils. The sedimentary facies of the Kitadani Formation is composed of meandering river channel and floodplain deposits. The paleogeographical reconstruction inferred that the Tetori Basin was located in the eastern margin of the Asian continent under cool climate. Based on invertebrate fossils, the Kitadani Formation is assigned to the Aptian age.

Cretaceous sediments in Thailand are composed mostly of non-marine deposits. The Khorat Group is the most fossiliferous strata in the Khorat Basin, and comprises six formations of the Triassic Nam Phong, the Jurassic–Cretaceous Phu Kradung, Phra Whian, Sao Khua, Phu Phan and Khok Kruat formations in ascending order. The uppermost Khok Kruat Formation, consisting of mainly reddish-brown siltstones and sandstones, has yielded abundant dinosaur remains. The sedimentary facies is referred as channel and bar, crevass-splay and floodplain. The Khorat Basin was located in the southern part of Asia under subtropical-tropical climate. The Khok Kruat Formation is assigned to the Aptian based on palynological data, the occurrences of the fresh water shark and the dinosaur fossils.

The Mesozoic terrestrial sequences in China are the Jehol, Hekou and Xinminpu groups. The Jehol Group is distributed in western Liaoning, northern Hebei and southeastern Inner Mongolia provinces, and consist mainly of weakly laminated to finely bedded tuffaceous sandstones and shales, intercalated with basalts and tuffs. Abundant tuffaceous horizons assigned the Jehol Group to the Barremian–Aptian age. The paleogeography of the Beipiao-Fuxin Basin for the Jehol Group is reconstructed as the highland in the 40°N under cool and semi-arid climate. The Hekou Group is distributed in the southern part of Gansu Province, and composed of 8 lithological units. The sedimentary facies are composed of alluvial fan, fan delta, fluvial, shore-shallow lake, semi-deep lake and delta plain. The sedimentary basin for the Hekou Group was placed in 31°N in western part of the Early Cretaceous of Asia. The assignment to the late Valanginian–Barremian age to this group is based upon the magnetostratigraphic and biostratigraphic results. The Xinminpu Group is distributed widely into the northern part of Gansu Province. This Group is divided into two formations of the

Xiagou Formation and Zhonggou Formation. I studied the Zhonggou Formation in the present study. The Zhonggou Formation overlies the Xiagou Formation with disconformity, and is mainly composed of mudstone and argillaceous sandstone in the lower unit and mudstones with horizontal bedding in the upper part. These sediments of the Xinminpu Group indicate the large lakes and surrounding braded-rivers depositional environments. The sedimentary basin of this group was located in 35°N of the central Asia. The geological age of the Xinminpu Group is assigned to the early Aptian–late Aptian (125/124–115Ma) based on paleontological and radiometric dating. In the Zhonggou Formation, the paleontological data of plants, invertebrates and vertebrates fossils (psittacosaurs and primitive neoceratopsians) suggest the Aptian–Albian as well.

(2) Four Early Cretaceous Asian iguanodontain taxa, three of them for re-description and one for new report, are described in this study. *Fukuisaurus tetoriensis*, one of two Japanese taxa from the Kitadani Formation, is positioned in the non-hadrosauriform styracosternan. New cranial elements such as prefrontal, frontal, angulars, and splenial are recognized. The maxilla, predentary and denary of this taxon shows a unique, and a combination of derived and primitive characters. *Koshisaurus katsuyama*, the other taxon, is derived iguandonontian at the basal Hadrosauroidea. Morphological traits of the maxilla are distinguishable from that of *Fukuisaurus*. Existence of the antorbital fossa on the maxilla of *Koshisaurus* settles this taxon in close to Gansu taxa.

Sirindhorna khoratensis was found from the Thailand, and the best-preserved ornithopod dinosaur in Southeast Asia. The holotype braincase has an rmophy on its extended sagittal crest to the frontoparietal suture of the skull. Based on the cladistics analysis, *S. khoratensis* was an affinity of Asian hadrosauroids.

New cranial specimen (ZMNH M8798) was collected from the Zhonggou Formantion (Albian) of the Xinminpu Group in Gansu Province, China. The most important character of ZMNH M8798 represents the existence of the antorbital fossa and bones forming this fossa. Comparing morphological characters to other iguanodonitans reveals that ZMNH M8798 is assigned to *Probactrosaurus gobiensis*. The phylogenetic analysis also supported this relationship. Descriptions of ZMNH M8798 include almost all cranial elements. Detail descriptions on each element are seldom done in non-hadrosaurid iguanodontians. ZMNH M8798, therefore, shed new light on morphologies of iguanodontian cranial bones.

(3) Based on the phylogenetic analysis on non-hadrosaurid iguanodontians, the 50% majority-rule consensus tree was proposed in the present study. European rhabdodons and zalmoxeses, and Australian *Muttaburrasaurus* form a monophyletic group at the most basal position of the Iguanodontia. Basal (non-styracosternan) ankylopollexians consists of mainly North American "*Camptosaurus*"-like taxa such as *Osmakasaurus depressus* and *Iguanacolossus fortis*. *Lanzhousaurus* is the most primitive taxon in Asia, and *Fukuisaurus* is one of primitive one among Asian ankylopollexian. Almost all other Asian iguanodontians

belongs to next clade Hadrosaurifomes, especially Hadrosauroidea containing all taxa derived from *Iguanodon* and *Mantellisaurus*. New specimen ZMNH M8798 from China is recovered as a sister taxon of *Probactrosaurus gobiensis*. The most primitive North American hadrosauroids (*Eolambia* and *Protohadros*) are included in the basal hadrosauromorpha.

4) The integrated studies of phylogenetic analysis, temporal data and paleogeological distributions of dinosaurs revealed dispersal patterns of the clade Iguanodontia in the Early Cretaceous. In the pre-Barremian, Asian iguanodontians (*Lanzhousaurus*) were strongly related to the European group, but not the North American one. Cosmopolitan distribution of iguanodontians in all continents had occurred during the Barremian–Aptian, suggesting connections of all continents in the northern hemisphere (Asia-Europe-North America). The invasion of Asian dinosaurs into the North America was presumably opened during the Barremian. However, the faunal connection between Asia and North America iguanodontian probably had been truncated until the Albian. In post-Albian, the hadrosauromorphans re-appeared in the North America. Thus, the distribution pattern of the Iguanodontia in the Early Cretaceous represents the connection/intermission between Asia and Europe or Asia and North America. These results suggest the possibility of Asian origin for the North American iguanodontians during the Early Cretaceous.